A COMPLEX OF CRYPTIC SPECIES IN THE GENUS *COPTODACTYLA* BURMEISTER (COLEOPTERA: SCARABAEIDAE: COPRINI)

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The *subaenea* species-complex in the coprine genus *Coptodactyla* Burmeister is described, comprising *C. nitida* Paulian, *C. papua* Lansberge, *C. subaenea* Harold and three new species, *C. matthewsi* and *C. storeyi*, from North Queensland, and *C. merdeka* from New Guinea. *Coptodactyla nitida* Paulian is removed from synonymy with *C. subaenea*. These externally almost identical species are primarily discriminated using sexual characters, namely the parameres, endophallus and vulvar sclerites. A phylogenetic analysis of the species complex is given. Five of the species are allopatric with respect to each other. Two sister species are widespread but allopatric in the Wet Tropics of North Queensland, where they meet at the Black Mountain Barrier, a known dry climate barrier at past periods of maximum aridity. A key is given for the 17 species of *Coptodactyla* and lectotypes are designated for *C. papua* and *C. subaenea*. ❐ *Coleoptera, Scarabaeidae, Coptodactyla, Australia, New Guinea, taxonomy, biogeography.*

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This paper revises a species-complex in the dung-beetle genus *Coptodactyla* Burmeister, which is abundant in the closed forests of north Queensland. The project is one of several initiated by the Co-operative Research Centre for Tropical Rainforest Ecology and Management, Cairns, which aim to provide a sound taxonomic and phylogenetic framework for the more significant genera of the Queensland Wet Tropics World Heritage Area. This survey of scarabaeine distribution and systematics has led to studies of diversity (Monteith, 1995) and area relationships within the Wet Tropics (Reid, Cranston & Reid, in press).

Such a project is feasible primarily thanks to the sound taxonomic base provided by Eric Matthews 27 ago (1972, 1974, 1976) and the subsequent efforts of project collaborators Geoff Monteith (Queensland Museum, Brisbane), Ross Storey (Department of Primary Industries, Mareeba) and Tom Weir (Australian National Insect Collection, Canberra), who have collected, curated and sorted 40,000 specimens of about 190 species (G. Monteith, pers. comm.) of Wet Tropics scarabaeines. Their collective resource provides an excellent platform for revisionary taxonomic studies.

Coptodactyla Burmeister is a genus of coprine scarabs (Montreuil, 1998) confined to Australia and New Guinea. The Australian species were comprehensively revised by Matthews, using male characters (Matthews, 1976). He had much less material available than the present author and did not examine the female genitalia or the male endophallus; examination of these structures has allowed more detailed discrimination of species and populations. This study has revealed six sibling species confused under the names *C. papua* Lansberge, *C. subaenea* Harold and *C. nitida* Paulian. No other taxonomic changes are necessary in the genus.

MATERIALS AND METHODS

Male genitalia were immersed in dilute KOH for several hours, then transferred to water. The parameres were removed from the basal piece, and the penis and endophallus extracted. The penis was separated from the endophallus by cutting the thin connecting membrane at the apex of the penis. The endophallic lobes were everted with fine forceps. The ejaculatory sac was not inverted as the sclerites were more clearly visible in the relaxed condition.

Female genitalia, including the vulvar sclerites, were removed from the apical abdominal ventrite, softened in dilute KOH, then water, and cleaned. The spermatheca was examined in glycerol.

Terminology largely follows Mathews (1976), with the following additions. Scarabaeines

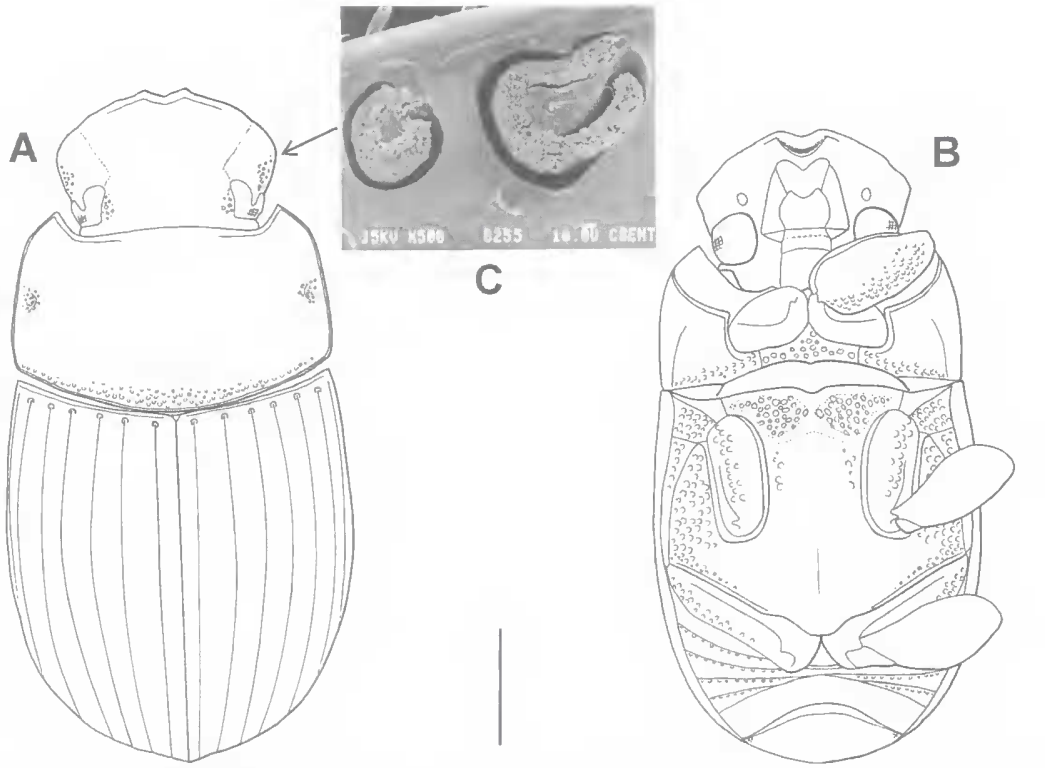

FIG. 1. *Coptodactyla subaenea* Harold, ♂, showing distribution of annular punctures. A, dorsum; B, venter; C, detail of annular punctures anterior to eye. Scale bar = 2mm.

commonly have patches of large annular punctures (Krikken, 1977) and the distribution of these is important for discriminating species in *Coptodactyla*. These punctures are deep (Fig. 1C), enclose setae, and may function as fungal storage pits for inoculating larval food. A nomenclature of male endophallic sclerites in Coprini is provided by Génier (1996), but this appears to be inappropriate for *Coptodactyla* species. The endophallus of all Australian species of the coprine genera *Coptodactyla* and *Thyregis* Blackburn has been examined. There are always three basal sclerites (Fig. 5B), in an ejaculatory sac, which form the sperm pump when everted: the flagellum, relatively short and stout and without divergent apices (flagella of Génier); the basal sclerite, a folded plate adjacent to the apical half of the flagellum; the ring sclerite, at or beyond the tip of the flagellum. Other areas of sclerotisation may be present (as in Fig. 5B), but when observed through the inverted wall are poorly defined and generally only lightly sclerotised. In *Coptodactyla* there is always a lateral sac (Fig. 5B), which may be further subdivided, branching off the base of the ejaculatory sac.

The female genitalia of *Coptodactyla* are unusual amongst Scarabaeinae in having extensive secondary sclerotisation around the vulva. The area immediately around the vulva is the vulvar sclerite (Fig. 9B), which may be lobed and asymmetrically folded. Between the vulvar sclerite and the anus there is usually a strongly sclerotised transverse bar, the dorsal sclerite, which may be derived from fusion of the hemisternites.

Seventeen hundred and fifty specimens of the *subaenea*-species complex were examined. Abbreviations for depositories are as follows: ANIC, Australian National Insect Collection, Canberra; BMNH, Natural History Museum, London; CMN, Canadian Museum for Nature, Ottawa; MCG, Museo Civici, Genoa; MZB, Museum Zoologicum Bogoriense, Bogor, Indonesia; DPIM, Queensland Department of Primary Industry, Mareeba; QM, Queensland Museum, Brisbane. The latitude and longitude for

Australian localities included in this revision are available from the Collection Manager, ANIC.

Abbreviations for collectors' names with more than one entry are as follows: GB, G. Bornemissza; EB, E.B. Britton; JGB, J.G. Brooks;DC, D.J. Cook; JF, J. Feehan; PF, P. Ferrar; HAH, H. & A. Howden; SM, S. Misko; GM, G. Monteith; GSM, G. & S. Monteith; CR, C.A.M. Reid; RS, R.I. Storey; GT, G.I. Thompson; AWH, A. Walford-Huggins; TW, T.A. Weir; DY, D. Yeates; PZ, P. Zborowski. Other abbreviations: Bch, Beach; C, Cape; Ck, Creek; I., Island; Mt, Mount/Mountain; NP, National Park; Pt, Point; Ra., Range; R., River; Rd, Road; Tbld, Tableland.

Descriptions are based on freshly emerged specimens, if available. Older specimens may have densely scratched and dull dorsal surfaces, and the oldest individuals have their protibiae reduced to pointed stumps and frontoclypeal anterior margins eroded.

Coptodactyla Burmeister, 1846

TYPE SPECIES. *Copris glabricollis* Hope, 1842, by monotypy (Matthews 1976).

DISTRIBUTION. Australia (coastal Queensland and Northern Territory) and New Guinea.

REMARKS. The genus was comprehensively described and its synonymy was discussed by Matthews (1976). The new species added below do not require any alteration to this description. Hitherto two species of this genus have been distinguished by the incomplete border (beading sensu Matthews) of the anterior edge of the pronotum. Here four additional species with this character-state are described and the whole group is placed in the *subaenea* species-complex.

Coptodactyla subaenea species-complex

DIAGNOSIS. Anterior border of pronotum medially effaced (Figs 1A, 2A-B); striae 8 and 9 complete to elytral base; males without secondary sexual modifications of head, pronotum or legs (Fig. 1); apices of parameres strongly deflexed (Fig. 2C-F); endophallus with one lateral sac (Fig. 5B).

DESCRIPTION. The following attributes are shared by all species of this complex and will not be repeated in the species descriptions (but note that some features may be obliterated or obscured in worn specimens).

Length 8-13.5mm, but rarely <9.5mm. Annular punctures, either circular or semicircular, distributed as follows (Fig. 1): sides of frontoclypeus anterior to eyes; inner margin of eyes; lateral pronotal pit; posterior margin of pronotum; posterior of prosternum; posterior of hypomeron internal to lateral groove; base of each stria; mesosternum; mesepimeron; sides and anterior of metasternum; metepisternum; hind margin of profemur; meso- and metacoxae; row across base of each ventrite except last; lateral angles of pygidium.

Head (Figs 1, 2A-B). Dorsum without ridges or horns in either sex; fronto-clypeal margin with slight notch at junction of gena, produced anteriorly as two upturned triangular lobes with median notch; downturned apex of clypeus almost triangular, with marginal arcuate groove for most of width (Fig. 1B); lateral (genal) angles blunt, sides contracted in straight line towards eyes; eye divided by narrow canthus for half of lateral length; eyes separated by 4-6 dorsal eye widths; most of anterior of frontoclypeus transversely rugose (wrinkled), head between eyes variably punctured, convex; antenna: length segment 1 at least equal to 2-6 combined, 2 elongate globular, 3 triangular, 3-6 increasing in width, 4-6 decreasing in length, width 6 twice length, 7-9 forming lamellate club, 7 shallowly excavate at base to house 6, 7-9 decreasing in width; last segment of maxillary palp fusiform, length 2-2.5x penultimate segment.

Thorax (Figs 1, 2A-B). Pronotum: anterior evenly convex, without excavation or tubercles, base with faint median longitudinal impression; sides of pronotum almost straight to shallowly curved; upper surface almost entirely punctured, more strongly at sides; anterior edge without border for middle eighth to third; two circular lateral median depressions present, connected to anterior angles by shallowly convex and often effaced ridge; hypomeron with long submarginal ridge c.0.75 length from base towards anterior excavation, impunctate except annular punctures; scutellum minute, size equal to pronotal sensory pit; elytra with 9 distinct deeply grooved, but feebly punctured (slightly foveolate), striae complete to base, stria 10 along edge of epipleuron, stria 9 fused to 10 one third from base; interstices flat except apical half of suture slightly convex and outer edge of elytron convex between striae 8 and 9, but without pseudepipleuron; meso- and metasterna completely fused; middle of metasternum shining, finely and sparsely punctured; wings fully developed; mid and hind trochanters with small tuft of dense stiff golden setae (may be abraded); male without

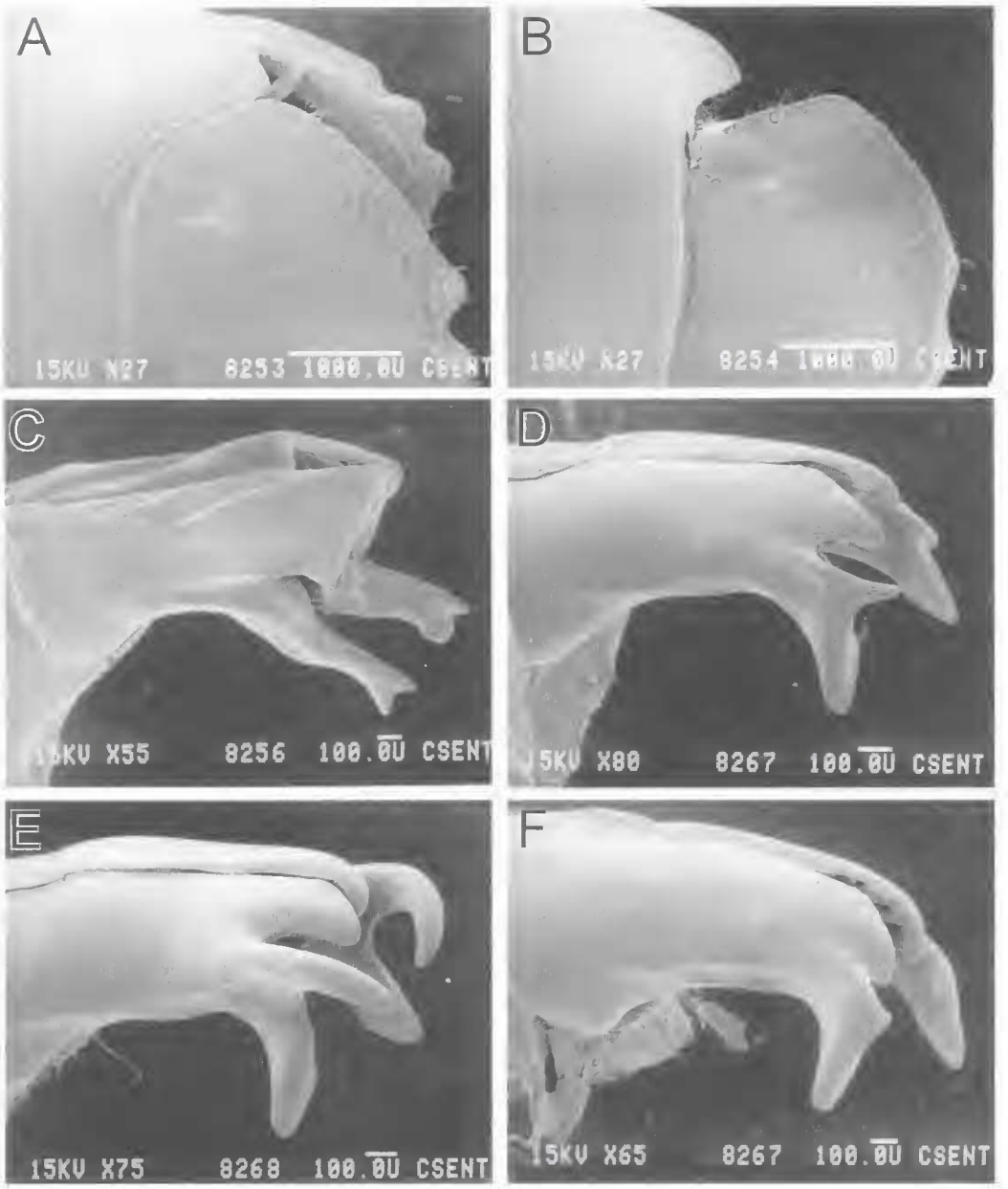

FIG. 2. *Coptodactyla* species. A-B, SEM left side head capsule: A, *matthewsi* (Iron Range); B, *nitida* (Broadwater Park); C-E, SEM apex of parameres: C, *matthewsi* (Iron Range); D, *nitida* (Cardwell Range); E, *storeyi* (Mount Webb); F, *subaenea* (McIlwraith Range).

secondary sexual characters on legs, femora with complete posterior marginal ridge, without median spur on fore tibia.

Male. Pygidium large, less than twice as broad as long (Fig. 7A), and apex last ventrite anteriorly excavate (Fig. 1B); genitalia: penis reduced to a deeply bilobed weakly sclerotised sheath (Fig.

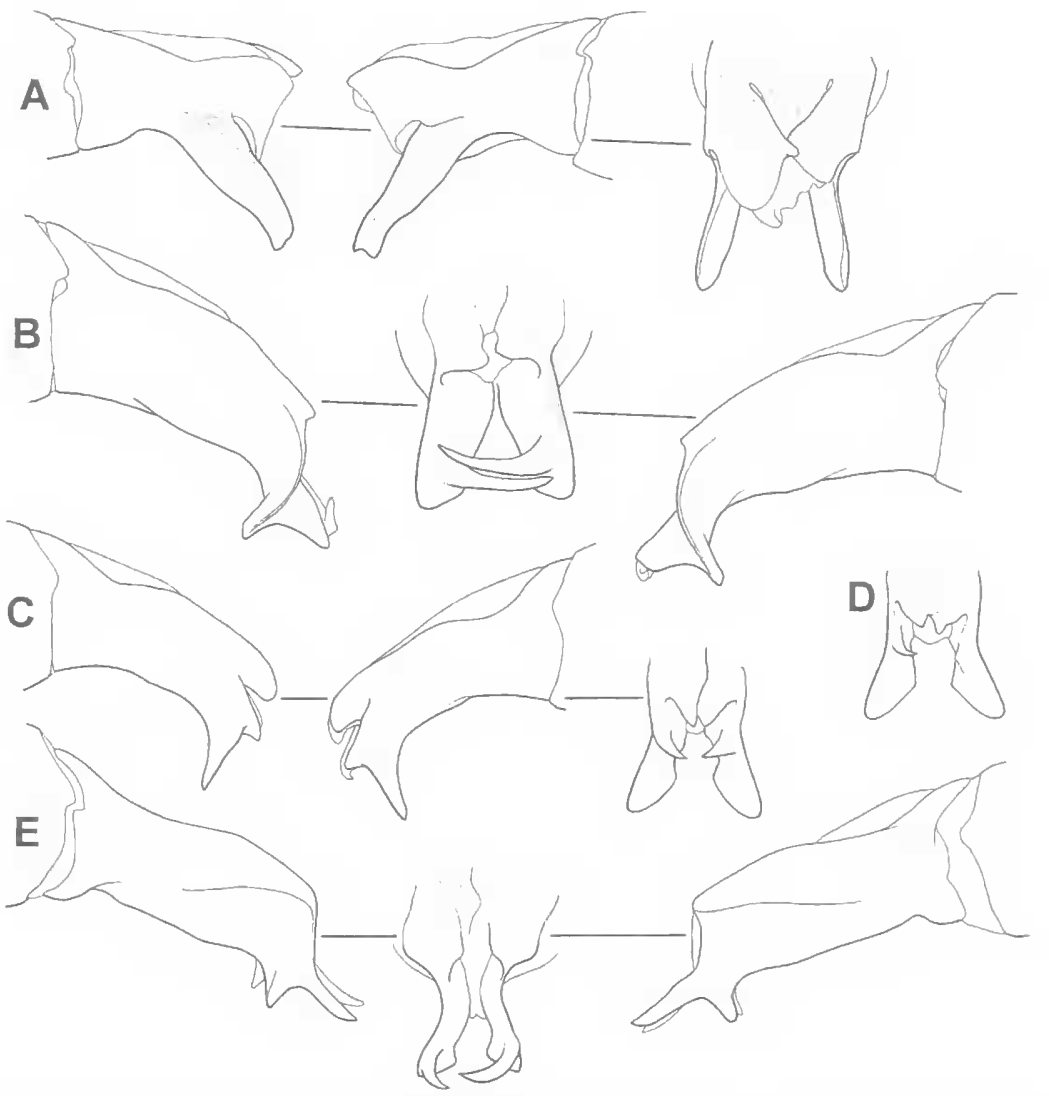

FIG. 3. *Coptodactyla* species, parameres, lateral, and apical: A, *matthewsi*; B, *merdeka*; C, *nitida* (Baldy Mountain); D, *nitida* (Paluma); E, *papua* (paralectotype). All to same scale.

5A); parameres (Figs 2C-F, 3, 4) symmetrical or almost so (rare individuals are asymmetric, Fig. 3D), apices reflexed and flattened, usually with a basal spur or tubercle; endophallus (Figs 5-6) with a single large lateral sac with patch of dense stiff spinules and usually a strongly sclerotised spine or bar; flagellum slightly curved; basal sclerite elongate rectangular, with various folds (almost identical in *C. nitida*, *C. storeyi* and *C. subaenea*); ring sclerite with two lobes, one more than twice length of other.

Female. Pygidium small, more than 2 × as broad as long (Fig. 7B), internal margin of apex deeply to shallowly excavate (Fig. 7C-11); apical margin of last ventrite evenly convex; genitalia: vulvar sclerites (Figs 8-9) either symmetrical or asymmetric, usually with broad dorsal plate; spermatheca approximately C-shaped, with weakly sclerotised 'window' at inner angle (Fig. 10).

REMARKS. *Coptodactyla depressa* Paulian, a species that does not belong to this complex, may

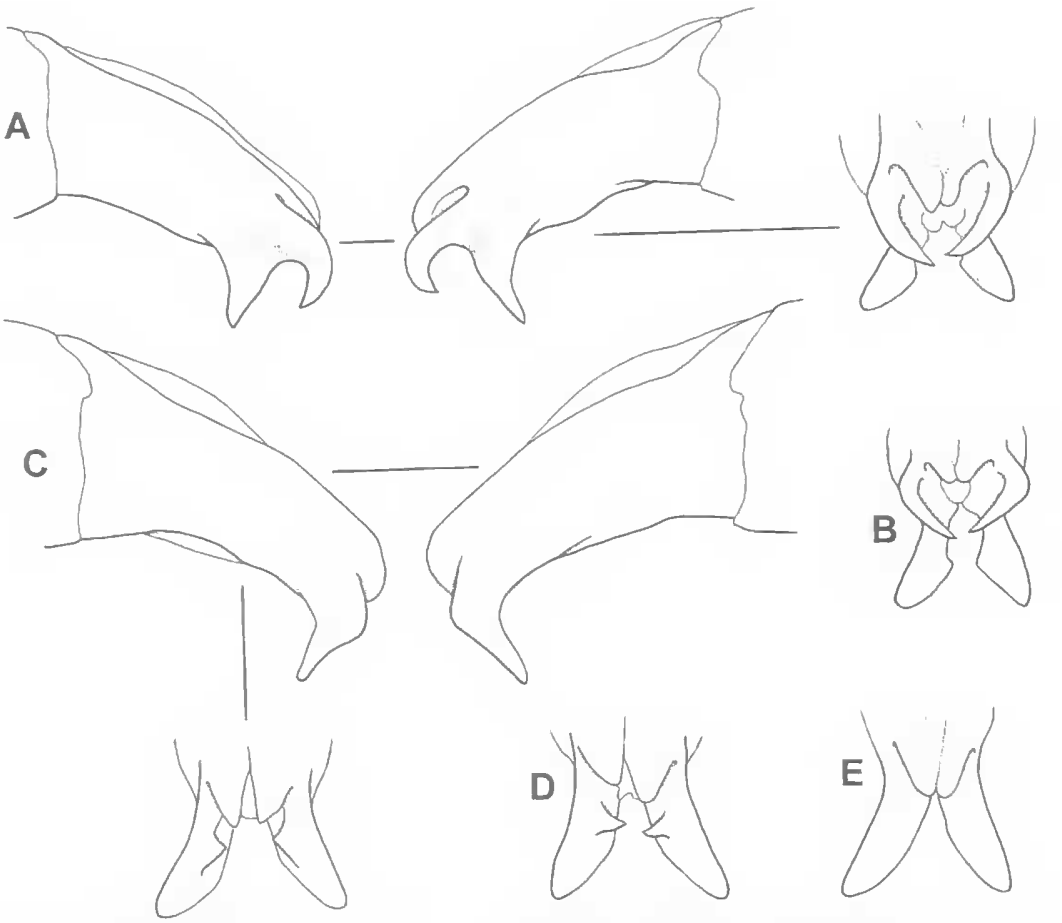

FIG. 4. *Coptodactyla* species, parameres, lateral, and apical: A, *storeyi* (Smithfield); B, *storeyi* (19km NE Mareeba); C, *subaenea* (Bald Hill); D, *subaenea* (paralectotype, Somerset); E, *subaenea* (Iron Range). All to same scale.

occasionally have the anterior pronotal border effaced in worn specimens, but can be distinguished by absence of striae 8 and 9 at elytral base, male with incomplete posterior femoral ridge, and female genitalia with dorsal sclerite reduced to an arched strut.

All species (for which there are biological data) in this complex are catholic in their choice of pabulum, being attracted to a range of decaying matter, not only faeces. Nesting biology has not been studied in this genus. All species are found in areas with at least high monsoonal rainfall, and adult activity is restricted to the rainfall months, at most from November to July, when there is softened soil. Thus late season specimens are generally more worn and duller than early season specimens. This seasonal pattern is also shown by the two species occuring in areas with continuous annual rainfall (*C. nitida* Paulian, *C. storeyi* sp. nov.), but neither is confined to such areas and both are found in a range of forest types. Only one species, *C. matthewsi* sp. nov., appears to be restricted to rainforest.

Coptodactyla matthewsi sp. nov.
(Figs 2A,C, 3A, 7C, 8A, 9A, 10A-B, 11)

ETYMOLOGY. Named for Eric Matthews, whose work has resolved the major taxonomic problems in the Australian Scarabaeinae.

MATERIAL. QUEENSLAND: Holotype, ♂: 11km NW Bald Hill, McIlwraith Ra., 13°44S 143°20E, search party

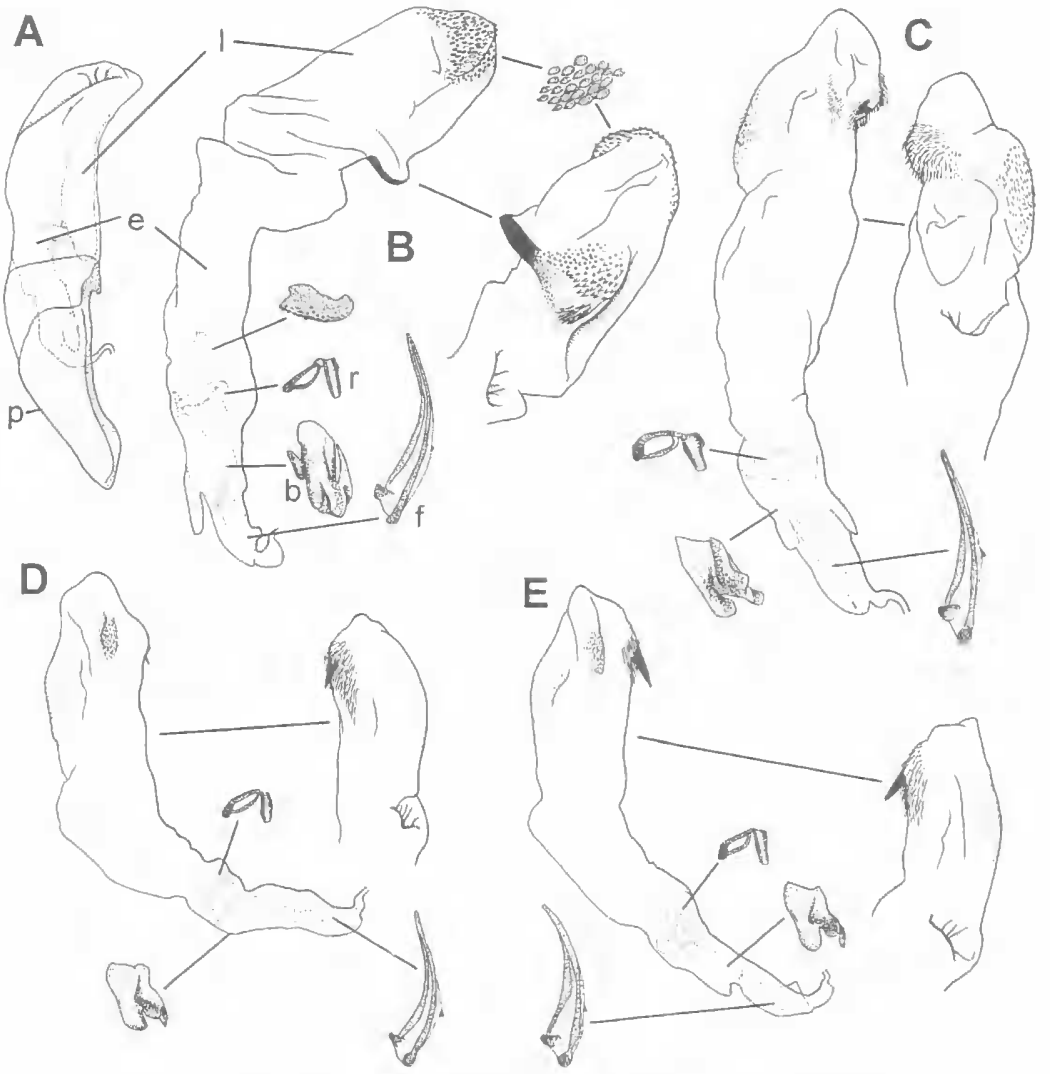

FIG. 5. Endophallus of *Coptodactyla* species. A, before removal of penis, B-E, after removal of penis and surrounding tissue and with lateral sac evaginated: A-B, *matthewsi* (Bald Hill); C, *merdeka*; D, *nitida* (Cardwell Range); E, *nitida* (Ravenshoe); b = basal sclerite; e = ejaculatory sac; f = flagellum; l = lateral sac; p = penis; r = ring sclerite. All to same scale.

campsite, human dung trap, closed forest, 520m, 27.vi-12.vii.1989, TW (ANIC). Paratypes (31) (* = specimen dissected): 2*, same data as holotype (ANIC); 3*, Iron Ra., rainforest, human dung trap, 15-21.iv.1977, RS (ANIC); 22*, Gordon's Mine area, Iron Ra., rainforest, 12-18.ii.1976, GM (QM); 2, Leo Ck Rd, McIlwraith Ra., 30km NE Coen, 500m, 29.vi-4.vii.1976, GSM (QM); 1*, West Claudie R., Iron Ra., 24.v.1974, AWH (CMN); 1, West Claudie R., Iron Ra., flight trap, rainforest, 3-10.xii.1985, GM & DC (ANIC).

DIAGNOSIS. Genal angles smooth or punctate, much more finely punctured than rugose anterior of frontoclypeus (Fig. 2A); pronotal hind angles and sides (lateral to pit and ridge) smooth and finely punctured or impunctate, without annular punctures; disc of elytra densely microreticulate; last ventrite with conspicuous annular punctures; apices of parameres with elongate, narrow, ventrally directed lobe (Figs 2C, 3A); endophallus

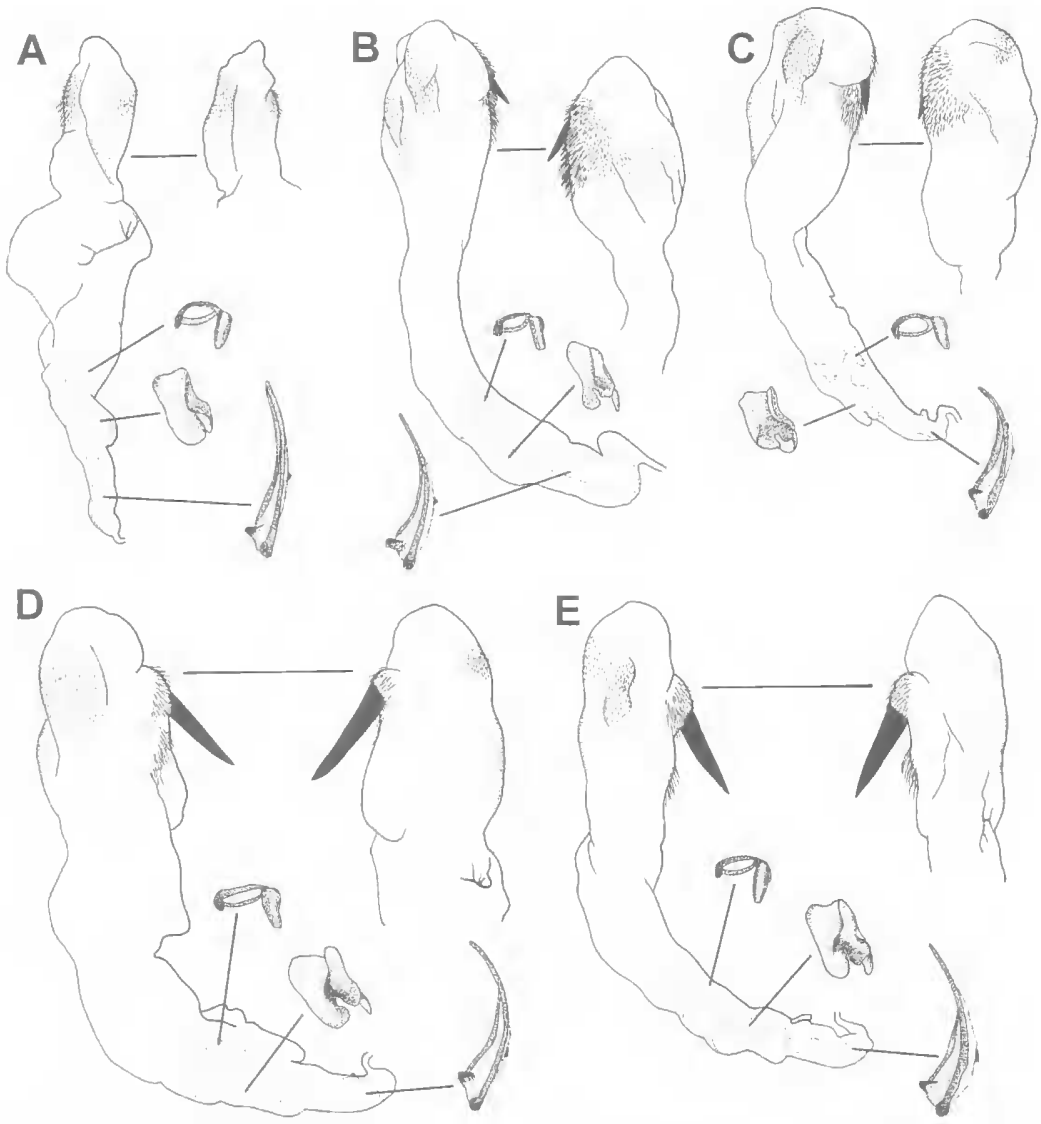

FIG. 6. Endophallus of *Coptodactyla* species, after removal of penis and surrounding tissue and with lateral sac evaginated: A, *papua*; B, *storeyi* (Mareeba); C, *storeyi* (Mount Cook); D, *subaenea* (Bamaga); E, *subaenea* (Bald Hill). All to same scale.

without apical spine on lateral sac (Fig. 5B); internal margin of female pygidium (Fig. 7C) with prominent inwardly directed lobes; ovipositor without dorsal sclerite; vulvar sclerite flat and symmetrical, without lobes (Figs 8A, 9A).

DESCRIPTION. Length: 10-13.5mm.

Head (Fig. 2A). Anterior of frontoclypeus wrinkled from line between lateral angles, except genal area finely punctured and smooth; posterior half of head increasingly finely and sparsely punctured to base, punctures much finer than pronotal disc; ventral clypeal groove shallow.

Thorax. Pronotum almost parallel-sided for most of length; pronotal disc moderately strongly punctured, interspaces 2-3 puncture diameters

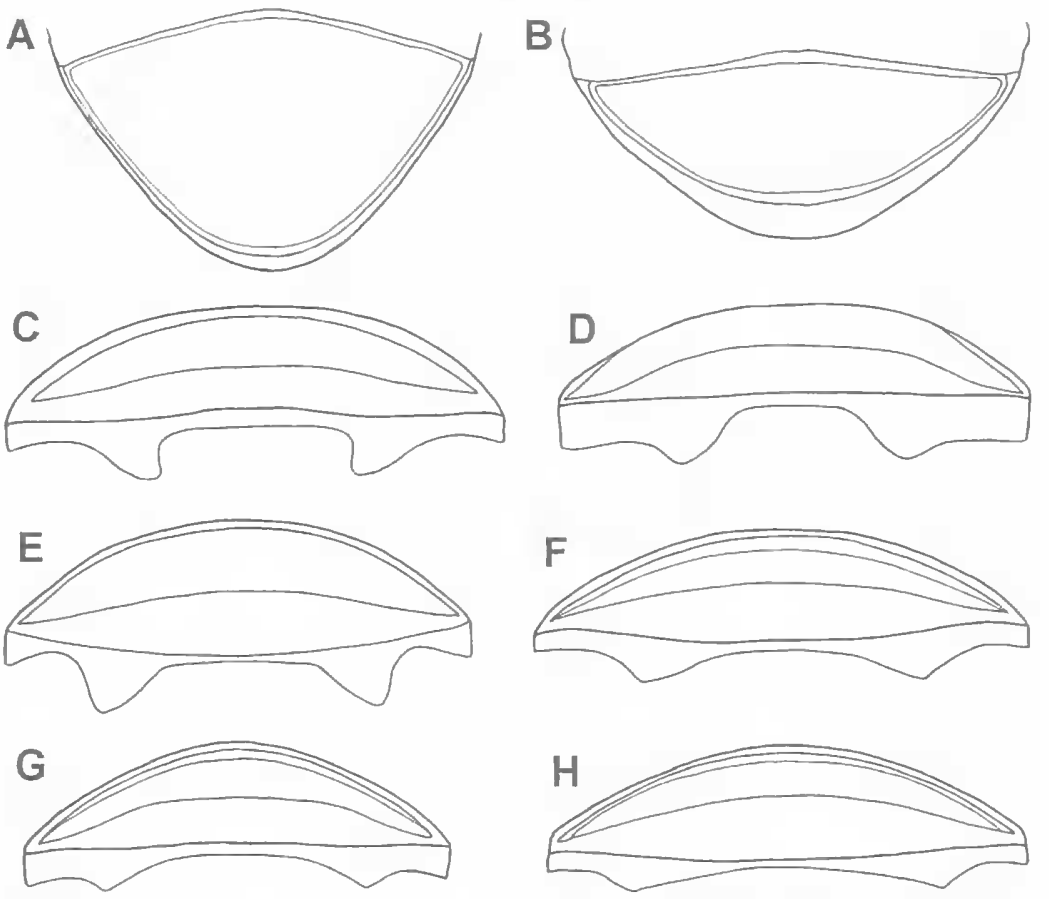

FIG. 7. *Coptodactyla subaenea*, pygidium: A, ♂; B, ♀; *Coptodactyla* species, apex of ♀ pygidium: C, *matthewsi*; D, *merdeka*; E, *papua*; F, *nitida*; G, *storeyi*; H, *subaenea*. All to same scale.

and finely micropunctate with faint microsculpture; hind angles and sides (lateral to pit and ridge) smooth and finely punctured or impunctate, without annular punctures; anterior border of pronotum lacking for 0.1-0.2× width of prothorax; elytra relatively convex in profile; elytra dull, strongly and densely microreticulate, except shining (less microsculptured), suture and 2-3 lateral intervals; elytral intervals minutely and sparsely punctured, more obviously at sides; ventral surfaces of mid and hind femora finely and sparsely punctured, without annular punctures.

Abdomen (Fig. 7C). Pygidium: male: shining, not microreticulate, minutely punctured; female: dull, strongly microreticulate, usually more evidently punctate; internal margin of female pygidium with prominent inwardly directed lobes; last ventrite with conspicuous annular punctures.

Male genitalia (Figs 2C, 3A, 5B). Apices of parameres produced as narrow straight lobes with bilobed tips: lateral sac with apical patch of stout scale-like spines, and median patch of fine spines at base of a large transverse sclerotised bar; flagellum relatively straight; basal sclerite strongly folded, with lateral lobes; secondary sclerite present in ejaculatory sac.

Female genitalia (Figs 8A, 9A, 10A-B). Dorsal sclerite absent or not strongly sclerotised; vulvar sclerite almost symmetrical, weakly sclerotised above genital opening, without erect lobe; spermatheca relatively small.

REMARKS. This species is known from isolated localities on the Iron and McIlwraith Ranges, central Cape York Peninsula (Fig. 11). There are no obvious morphological differences between

the populations, which may be continuous through this rugged country. It is entirely sympatric with *C. subaenea*. All specimens were collected in rainforest, at human dung and in flight traps. Collection dates include most months from December to July, which is the monsoonal wet season.

Coptodactyla merdeka sp. nov.
(Figs 3B, 5C, 7D, 9B, 10C, 11)

ETYMOLOGY. The species name means freedom in Indonesian.

MATERIAL. INDONESIA.WEST PAPUA. Holotype, ♂: New Guinea exped., Mamberamo R., Pionierbivak, xii.1920, van Heurn (MZB). Paratypes (15): 2 ♀: same data as holotype (ANIC); 13, Timika, Freeport Concession, Irian Jaya, 11.iii.1997, R. Ubaidillah (ANIC, MZB).

DIAGNOSIS. Externally identical to *C. papua* Lansberge: pronotal hind angles and sides (lateral to pit and ridge) punctured and bordered by large annular punctures; disc of elytra not microreticulate; last ventrite with conspicuous annular punctures; parameres (Fig. 3B) without elongate lateral excavation, not laterally ridged, apices with large inwardly directed, overlapping, slightly curved spurs; lateral sac of endophallus with minute subapical sclerite (Fig. 5C); ovipositor (Fig. 9B) dorsal sclerite sharply transversely ridged, the ridge convex; vulvar sclerite approximately symmetrical, without projecting lobe; spermatheca (Fig. 10C) significantly larger than in other species.

DESCRIPTION. Length 9.5-13mm.

Head. Anterior of frontoclypeus wrinkled from line between anterior margins of eyes, except genal area strongly punctured, not wrinkled; posterior half of head moderately strongly and closely punctured, punctures stronger than on pronotal disc; ventral clypeal groove deep.

Thorax. Pronotum rounded at sides; pronotal disc finely and sparsely punctured, interspaces 3-5 puncture diameters, micropunctate but shining, without microsculpture, punctures larger and closer towards sides, separated by 1-2 diameters; hind angles and sides (lateral to pit and ridge) punctured and bordered by large annular punctures; anterior border of pronotum lacking for 0.2× width of prothorax; base of lateral part of hypomeron with one or more annular punctures; elytra relatively flat in profile; elytra shining, not microreticulate, intervals finely and sparsely punctured, not more obviously at sides; ventral surfaces of mid and hind femora with numerous annular punctures and large punctures.

Abdomen (Fig. 7D). Pygidium: shining, not microreticulate, disc finely punctured to impunctate; last ventrite with conspicuous annular punctures; internal margin of female pygidial apex deeply excavate.

Male genitalia (Figs 3B, 5C). Parameres without elongate excavation, not laterally ridged, apices flat and strongly deflexed, with long, inwardly directed, overlapping, slightly curved spurs; lateral sac of endophallus with a dense median brush of small stiff spines around small flat sclerite; flagellum relatively straight; basal sclerite quadrangular, with strong median fold and basal lobes.

Female genitalia (Figs 9B, 10C). Dorsal sclerite sharply transversely ridged, ridge convex; vulvar plate almost symmetrical, generally weakly sclerotised, produced above genital opening as a weak ridge; spermatheca relatively large, C-shaped.

REMARKS. This species is known from 16 specimens collected in West New Guinea (Fig. 11), 3 of which had been identified as *C. papua* by Gillet in 1925. The specimens taken at Timika were collected at 100m, in 'dry lowland forest'. The habitat at the lowland riverplain of Pionierbivak is unknown.

Coptodactyla nitida Paulian, stat. rev.
(Figs 2B,D, 3C-D, 5D-E, 7F, 8B, 9C-D, 10D-E, 12)

Coptodactyla nitida Paulian 1933: 70; Matthews 1976: 32, jun. syn. of *C. subaenea* Harold.

MATERIAL. QUEENSLAND: Holotype, ♀: Nov.Holl.Queensld, Fry coll. 1905-100 (BMNH). OTHER MATERIAL. (951) (* = specimen dissected; label data abbreviated to site, altitude, date & collector): QUEENSLAND: 88*, Atherton, 7.v.1964, 23-26.iii.1965, 9-12.ii.1975, Bornemissza, HAH (ANIC, CMN); 1, 4mi. S Atherton, 18.ii.1975, HAH (CMN); 3, Bally Knob, 1100m, 6.xii.1998-6.ii.1999, GM & DC (QM); 95*, Baldy Mt. Rd, 860m, 1120-1130m, 30.xi.1997-12.ii.1998, 3-6.ii.1999, GM & DC (QM); 1, Balgal Bch, 5m, 4-12.ii.1998, GM & DC (QM); 1*, Bilyana, 30m, 4-12.ii.1998, GM & DC (QM); 1*, Broadwater Park, 35km NW Ingham, 22.xii.1986, Hamlet (QM); 11, Cardwell Gap, 120m, 4-12.ii.1998, GM & DC (QM); 7, 5km N Cardwell Gap, 10m, 4-12.ii.1998, GM & DC (QM); 10*, Cardwell Ra., 2.v.1964, GB (ANIC); 26, Crystal Ck, 20.iii.1965, GB (ANIC); 40*, Damper Ck, 10m, 4-12.ii.1998, GM & DC (QM); 1, Five Mile Ck, 10m, 16-25.iv.1999, CR (ANIC); 141*, Gillies Hwy, Heales Lookout, 30.iii.1965, 7.v.1969, GB, PF (ANIC); 1, 3mi N Herberton, 14.ii.1976, RS (DPIM); 1*, 7mi SW Herberton, 6.xii.1968, EB (ANIC); 14*, Hinchinbrook I.,

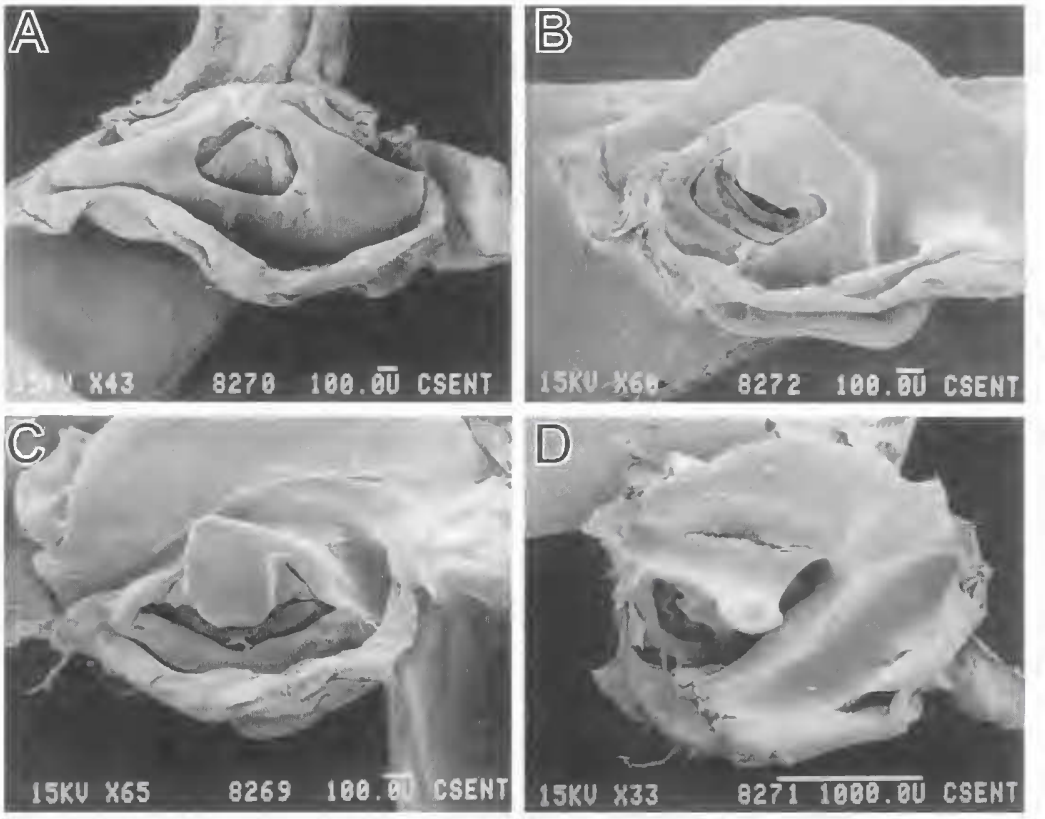

FIG. 8. *Coptodactyla* species, SEM vulvar sclerites: A, *matthewsi* (Iron Range); B, *nitida* (Paluma); C, *storeyi* (Mount Cook); D, *subaenea* (McIlwraith Range).

Gayundah Ck, 10m, 8-18.xi.1984, GM, GT & DC (QM); 1*, 19km N Ingham, 25-26.ii.1976, RS (DPIM); 4, Kirrama, Cardwell Ra., 600m, 25.iv.1997, CR (ANIC); 31, Kirrama Ra., 700m, 4.ii.1970, 29.xii.1986, Ey, HAH (ANIC, CMN); 14*, Little Crystal Ck, 30.v.1969, PF, Huppatz (ANIC); 9, Mill Ck, 940-1030m, 5-9.ii.1999, GM & DC (QM); 24*, Millstream Falls, 1040m, 5-7.xii.1998, 4-9.ii.1999, GM & DC (QM); 6*, Mt Collins, Cardwell Ra., 26-27.iv.1997, CR (ANIC); 1, Mt Haig, 17-21.iv.1994, Morse (ANIC); 1, Mt Speculation, 4.i.1967, JGB (ANIC); 87, Paluma, 20.iii.1965, GB (ANIC); 28, 5mi E Paluma, Saddle Camp, 1700', 14.v.1969, 18.i.1970, GB, EB & SM (ANIC); 1, 14km N Paluma, 850m, 11.ii.1971, JGB (ANIC); 5, c6km W Paluma, 9-11.i.1969, JGB (ANIC); 53*, c.9km W Paluma, 2600-2900', 16-18.i.1970, 4-13.xii.1973, 10.i.1989, EB, SM, JGB, RS (ANIC, DPIM); 18*, c12km W Paluma, 11.i.1964, 9-11.i.1969, 10.i.1989, JGB, HAH (ANIC, CMN); 1, 7mi NNE Ravenshoe, 22.iv.1969 (ANIC); 70, 2-3km SW Ravenshoe, 860-880m, 5-7.xii.1998, 3-8.ii.1999, GM (QM); 48, 3km SE Ravenshoe, 960m, 5-11.ii.1998, 4-6.ii.1999, GM & DC (QM); 1*, 4km SSE Ravenshoe, 920m, 5-11.ii.1998, GM & DC (QM); 1, 2-17mi W Ravenshoe, 1.iv.1968, Matthews (ANIC); 3*, Tully, 3.v.1965, GB (ANIC); 1, 5mi W Tully, 23.iv.1955, Norris & Common (ANIC); 29*, 2km SW Tully Falls, 760m, 2.xii.1998-4.ii.1999, GM & DC (QM); 36, 2.5km NW-3.5km N Tumoulin, 980-1020m, 4-5.ii.1999, GM, DC (QM); 12*, Wallaman Falls, 620m, 5-12.ii.1996, GM (QM); 2*, Watsonville, 7-14.ii.1976, RS (DPIM); 1*, Webster Rd, Evelyn, 990m, 5-11.ii.1998, GM & DC (QM); 18, 2km SSE Wondecla, 910m, 3-6.ii.1999, GM & DC (QM); 2, Yungaburra, 27.iii.1965, GB (ANIC).

DIAGNOSIS. Externally identical to *C. subaenea* Harold and *C. storeyi* sp. nov.: pronotal hind angles and sides (lateral to pit and ridge) smooth and finely punctured, without annular punctures; disc of elytra not microreticulate; last ventrite impunctate, without conspicuous annular punctures; apical lobes of parameres (Figs 2D, 3C-D, 12) with sharp incurved short spine; lateral sac of endophallus (Fig. 5D-E) with small apical spine, 0.3-0.5× width of sac, less densely spiculate at base of this than *C. storeyi*; vulvar sclerite (Figs 8B, 9C-D) asymmetric with small rounded projecting lobe.

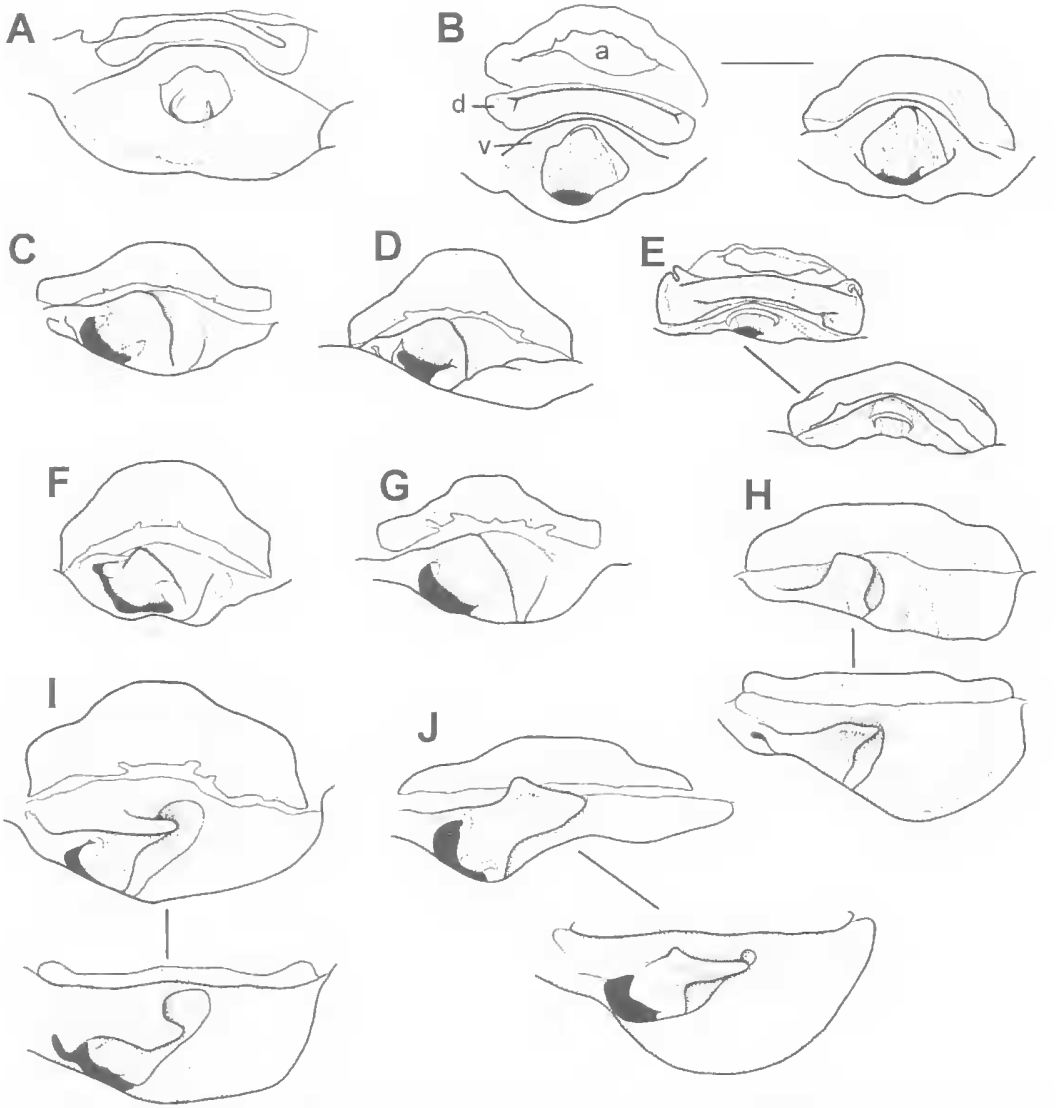

FIG. 9. *Coptodactyla* species, vulvar sclerites: A, *matthewsi* (Bald Hill); B, *merdeka*; C, *nitida* (holotype, Queensdland); D, *nitida* (Gillies Highway); E, *papua*; F, *storeyi* (Mount Cook); G, *storeyi* (Black Mountain); H, *subaenea* (paralectotype, Somerset); I, *subaenea* (Mount Tozer); J, *subaenea* (Heathlands); a = anus; d = dorsal sclerite; v = vulvar sclerite. All to same scale.

DESCRIPTION. Length: 8-12.5mm.

Head (Fig. 2B). Anterior of frontoclypeus wrinkled from line between anterior margins of eyes, including genal angles; posterior half of head moderately strongly and closely punctured, punctures similar to pronotal disc; ventral clypeal groove deep.

Thorax (Fig. 2B). Pronotum rounded at sides; pronotal disc strongly punctured, interspaces 1-2 puncture diameters, micropunctate but shining, without microsculpture, punctures finer and sparser at base; hind angles and sides (lateral to pit and ridge) smooth and finely punctured, without annular punctures; anterior border of pronotum lacking for 0.25-0.4× width of prothorax; base

of lateral part of hypomeron without annular punctures; elytra relatively flat in profile; elytra shining, not microreticulate, intervals finely and sparsely punctured, not more obviously at sides; apical half of ventral surfaces of mid and hind femora with annular punctures and fine punctures.

Abdomen (Fig. 7F). Pygidium: shining, not microreticulate, disc finely punctured to impunctate; last ventrite impunctate, without conspicuous annular punctures; internal margin of female pygidial apex shallowly excavate.

Male genitalia (Figs 2D, 3C-D, 5D-E). Apices of parameres strongly deflexed as a flat lobe with sharp inwardly directed triangular tubercle or curved spur at base; lateral sac with dense patch of stiff spines at base of relatively short black spine, less than half width of sac; flagellum relatively curved; basal sclerite quadrangular, with strong median fold and basal lobes.

Female genitalia (Figs 8B, 9C-D, 10D-E). Dorsal sclerite flat and broad, without sharp transverse ridge; vulvar sclerite strongly asymmetric, produced above genital opening as a smoothly rounded lobe; spermatheca relatively small.

Intraspecific variation. The size of the spines on the apex of the parameres does not vary clinally (Fig. 12) but may vary between parameres (Fig. 3D). In all specimens the spines are inwardly directed and appear as a triangular process in profile. The spine of the endophallus varies in size (Figs 5D-E), overlapping with that of *C. storeyi*, but the basal patch of spicules is generally less extensive. The shape of the vulvar plate varies slightly (Figs 8B, 10D-E), but the lobe is consistently less angular than in *C. storeyi*.

REMARKS. Paulian distinguished *C. nitida* by its shining upper surface, but this is characteristic of all freshly emerged specimens of *Coptodactyla* species (except *C. matthewsi*), which become extremely scratched and dull with age. The female holotype has been dissected to confirm its identity (Fig. 9C).

The species is the southernmost member of the *subaenea*-complex, found from just south of Mareeba on the Atherton Tableland, to Bluewater State Forest at the southern end of the Paluma Range (Hill 1993, as *C. subaenea*), from 5 to 1120m above sea level (Fig. 12). It is entirely allopatric with respect to the neighbouring *C. storeyi*, although the two species occur within 5km of each other, south-east of Mareeba. Hill (1996) noted that *C. nitida* (as *C. subaenea*) is nocturnal, attracted to light, characteristic of open *Eucalyptus* and *Allocasuarina* forest but also occuring in rainforest, and found at a variety of baits (mushroom, liver, dung, banana). Specimens I have seen were collected in open woodland or wet sclerophyll (tall eucalypt) forest, rarely rainforest, in areas of relatively high rainfall, at dead fish, fungi, human or cow dung, or at light and in flight traps. This species has been collected in every month from November (once) to May, which is the duration of the monsoonal wet season.

Coptodactyla papua Lansberge
(Figs 3E, 6A, 7E, 9E, 10F, 11)

Coptodactyla papua Lansberge 1885: 393

MATERIAL. Lectotype (here designated), ♂: PAPUA NEW GUINEA: labelled: 'Nuova Guinea, Fly River, 1876-77, L. M. D'Albertis' and 'syntypus *Coptodactyla papua* Lansberge, 1885', (MCG). Paralectotypes (3): ♂, 2♀, same data as lectotype (MCG). Lansberge (1885) did not indicate how many specimens were available to him. The types listed here are labelled 'syntypus, *Coptodactyla papua* Lansberge, 1885' and two are additionally labelled 'typus'.

DIAGNOSIS. Externally identical to *C. merdeka*; pronotal hind angles and sides (lateral to pit and ridge) punctured and bordered by large annular punctures; disc of elytra not microreticulate; parameres laterally ridged above elongate excavation, apices flat and strongly deflexed, with large projecting and only slightly incurved basal spurs (Fig. 3E); lateral endophallic sac without subapical spine (Fig. 6A); ovipositor dorsal sclerite (Fig. 9E) sharply transversely ridged, ridge shallow and angular; vulvar sclerite approximately symmetrical, without projecting lobe.

DESCRIPTION. Length 10.5-11.5mm.

Head. Anterior of frontoclypeus wrinkled from line between anterior margins of eyes, except genal area strongly punctured, not wrinkled; posterior half of head moderately strongly and closely punctured, punctures stronger than on pronotal disc; ventral clypeal groove deep.

Thorax. Pronotum rounded at sides; pronotal disc finely and sparsely punctured, interspaces 3-5 puncture diameters, micropunctate but shining, without microsculpture, punctures larger and closer towards sides, separated by 1-2 diameters; hind angles and sides (lateral to pit and ridge) punctured and bordered by large annular punctures; anterior border of pronotum lacking for 0.2 × width of prothorax; base of lateral part of hypomeron with one or more annular punctures; elytra relatively flat in profile; elytra

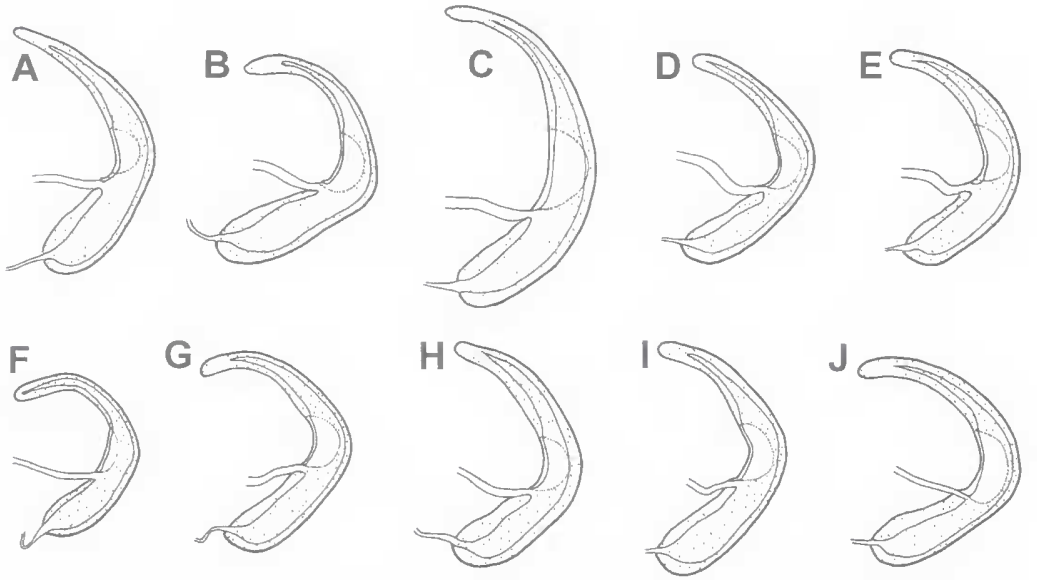

FIG. 10. *Coptodactyla* species, spermatheca: A, *matthewsi* (Iron Range); B, *matthewsi* (Bald Hill); C, *merdeka*; D, *nitida* (Gillies Highway); E, *nitida* (Paluma); F, *papua*; G, *storeyi* (Mount Lewis); H, *storeyi* (Mount Cook); I, *subaenea* (Bald Hill); J, *subaenea* (Mount Tozer). All to same scale.

shining, not microreticulate, intervals finely and sparsely punctured, not more obviously at sides; ventral surfaces of mid and hind femora with numerous annular punctures and large punctures.

Abdomen (Fig. 7E). Pygidium: shining, not microreticulate, disc finely punctured to impunctate; last ventrite with conspicuous annular punctures; internal margin of female pygidial apex deeply excavate.

Male genitalia (Figs 3E, 6A). Paramcres laterally ridged above elongate excavation, apices flat and strongly deflexed, with large projecting and only slightly incurved basal spurs (Fig. 4D); lateral sac of endophallus with a dense median brush of small stiff spines, without strongly sclerotised spine; flagellum relatively straight; basal sclerite quadrangular, with strong mcdian fold and basal lobes.

Female genitalia (Figs 9E, 10F). Dorsal sclerite sharply transversely ridged, but stout, about as broad as deep; vulvar plate almost symmetrical, generally weakly sclerotiscd, produced above genital opening as a weak ridge; spermatheca relatively small, strongly C-shaped.

REMARKS. This species is known from just the four type specimens, habitat unknown. They were collected by D'Albertis in either November-December 1875 or May-July 1876, within 580km of the mouth of the Fly River (Goode, 1977) (Fig. 11).

Coptodactyla storeyi sp. nov.
(Figs 2E, 4A-B, 6B-C, 7G, 8C, 9F-G, 12)

ETYMOLOGY. This species is named for Ross Storey, as thanks for help rendered and in recognition of his contribution to knowledge of Australia's tropical Coleoptera..

MATERIAL. QUEENSLAND: Holotype, ♂ (QMT 93003, in QM): Hann Tbld (north end), 16°49S 145°11E, pitfalls, open forest, 950m, 11-13.xii.1995, GM. Paratypes (367): (* = specimen dissected; label data abbreviated to site, altitude, date & collector): 4, Abbatoir Swamp, 350m, 24-25.xi.1998, GM (QM); 12*, same data as holotype (QM); 3*, Bakers Blue Mt., 17km W Mt Molloy, 1100m, 30.xii.1989-18.i.1990, GM (QM); 1*, Black Mt. Rd, c.17km N Kuranda, 12.v.1970, JGB (ANIC); 9, 1km NW Buchan Pt, 5m, 14-18.v.1998, 11-13.ii.1999, GM (QM); 1*, C. Tribulation, 10m, 12-15.vii.1982, S. & J. Peck (ANIC); 6*, 47km NE [sic, by road] Cooktown, 23.xii.1979, RS (ANIC, DPIM); 1*, 16km up Davies Ck Rd, 18.i-2.ii.1983, RS & Titmarsh (DPIM); 2*, Davies Ck, 21.ii.1981, RS (DPIM); 2*, Douglas Ck, 15km SE Mareeba, 630m, 6-10.ii.1998, GM & DC (QM); 3, Emmagen Ck, 10m, 17-19.xi.1998, GM (QM); 32*, Hann Tbld, 13km WNW Mareeba, 17.ii-20.iii.1989, 5.xi-8.xii.1993, 8.xii.1993-13.i.1994, 1.iii-12.iv.1994, RS, Dickinson, De Faveri (DPIM); 3*, Hann Tbld, north end, 950-1000m, 11-14.xii.1995, GM, GT & DC (QM); 31, Hann Tbld, 3km SSW Tower, 700m, 26-27.xi.1998, GM

(QM); 17, ditto, Radar Station, 950m (QM); 44, 2.5-4km S Hartleys Ck, 5-10m, 14-18.v.1998, 3-11.ii.1999, GSM, DC (QM); 4*, Hazelmere Station, 24km WNW Cooktown, 8.v.1981, JF (ANIC); 1*, Home Rule area, 300-400m, 7-8.i.1991, GM (QM); 3, 14km NW Hope Vale Mission, 7-10.v.1981, JF (ANIC); 1*, Julatten, 10.iv.1978, AWH (CMN); 1, 9km NE Julatten, 26.xii.1986-8.i.1987, HAD (CMN); 1*, 2km ENE Kuranda, 360m, 19-21.iv.1999, CR & I. Reid (ANIC); 1*, 19km NE Mareeba, 12.ii-20.iii.1985, RS & Halfpapp (DPIM); 5*, 19.5km ESE Mareeba, 24.xii.1986, 3.i.1987, RS (DPIM); 3*, Mary Ck, 5.xii.1968, EB & SM (ANIC); 1*, Mt Cook NP, 10-12.v.1981, JF (ANIC); 1, Mt Finnigan, 37km S Cooktown, 850-1100m, 19-22.iv.1982, GM, DY & DC (QM); 24, 4km WNW Mt Molloy, 350m, 24-25.xi.1998, GM (QM); 2, Mt Webb, 10.v.1986, Holm (ANIC); 12*, 3km NE Mt Webb, 30.iv-3.v.1981, JF (ANIC); 9, Noah Bch, 10m, 26.xii.1997-7.i.1998, Grove (QM); 4, Oak Bch, 5m, 3-11.ii.1999, GM & DC (QM); 4, 4.5km W Port Douglas, 10m, 3-11.ii.1999, GM, DC (QM); 4*, top of Quaid Rd, 5.i-9.ii.1998, DeFaveri & Halfpapp (DPIM); 11, Rex Ra., 50-90m, 15-18.v.1998, 3-11.ii.1999, GSM, DC (QM); 9*, Shiptons Flat, 220m, 19-22.xi.1998, GM (QM); 13*, Smithfield, 20m & 100m, vi.1997, 3-4.i.1998, CR (ANIC); 29*, Upper Station Ck, 350-370m, 6-9.ii.1998, 23-25.xi.1998, 3-11.ii.1999, GM & DC (QM); 51*, Windsor Tbld, 28km NNW Mt Carbine, 850-900m, 15-18.iv.1982, 20.xii.1985-15.i.1986, 25.xi.1997-9.ii.1998, 9.ii-17.v.1998, RS, Brown, GM, DC, DY (DPIM, QM).

DIAGNOSIS. Externally identical to *C. subaenea* Harold and *C. nitida* Paulian: hind angles and sides (lateral to pit and ridge) smooth and finely punctured, without annular punctures; disc of elytra not microreticulate; apical lobes of parameres with large projecting and down-curved spine (Figs 2E, 4A-B, 12); lateral sac of endophallus (Fig. 6B-C) with small to moderately long apical spine, 0.3-0.5 × sac width and larger patch of basal spicules than *C. nitida*; last ventrite impunctate, without conspicuous annular punctures; vulvar sclerite (Figs 8C, 9F-G) asymmetric with small, angular, projecting lobe.

DESCRIPTION. Length: 8.5-13mm.

Head. Anterior of frontoclypeus wrinkled from line between anterior margins of eyes, including genal angles; posterior half of head moderately strongly and closely punctured, punctures similar to pronotal disc; ventral clypeal groove deep.

Thorax. Pronotum rounded at sides; pronotal disc strongly punctured, interspaces 1-2 puncture diameters, micropunctate but shining, without microsculpture, punctures finer and sparser at base; hind angles and sides (lateral to pit and ridge) smooth and finely punctured, without annular punctures; anterior border of pronotum lacking for 0.25-0.4 × width of prothorax; base of lateral part of hypomeron without annular punctures; elytra relatively flat in profile; elytra shining, not microreticulate, intervals finely and sparsely punctured, not more obviously at sides; apical half of ventral surfaces of mid and hind femora with annular punctures and fine punctures.

Abdomen (Fig. 7G). Pygidium: shining, not microreticulate, disc finely punctured to impunctate; last ventrite impunctate, without conspicuous annular punctures; internal margin of female pygidial apex shallowly excavate.

Male genitalia (Figs 2E, 4A-B, 6B-C, 12). Apices of parameres strongly deflexed as a flat lobe with large strongly curved spur at base, directed obliquely inwards; lateral sac with dense brush of fine stiff spicules around a large black spine, less than half width of sac; flagellum relatively curved; basal sclerite quadrangular, with strong median fold and basal lobes.

Female genitalia. Dorsal sclerite flat and broad, without sharp transverse ridge; vulvar sclerite strongly asymmetric, produced above genital opening as a right-angled or more acute, generally triangular, lobe (Figs 3A, 9F-G); spermatheca relatively small (Fig. 10G-H).

Intraspecific variation. The large apical spines on the parameres are relatively uniform in size across the range of *C. storeyi*, constantly strongly curved and down-turned in profile (Figs 2E, 4A-B, 12). The lobe of the vulvar sclerite varies in shape, but is always angulate (Figs 8C, 9F-G). The subapical spine of the lateral endophallic sac (Fig. 6B-C) varies in size, overlapping with *C. nitida*, but the patch of basal spiculae is generally larger.

REMARKS. The species occurs from just south of Mareeba at Davies Creek north to Cape Flattery (Fig. 12). It is entirely allopatric with respect to the neighbouring *C. nitida*, although the two species occur within 5km of each other, though at different altitudes, southeast of Mareeba. *Coptodactyla storeyi* has been collected from horse, cow and human dung, dead fish, fungi, flight intercept traps and at light. It commonly occurs in rainforest, but also *Eucalyptus* and *Allocasuarina* open forest, in areas of relatively high rainfall, from 5 to 1100m above sea level. The species has been collected in every month from December to May, and July (once).

Coptodactyla subaenea Harold
(Figs 1, 2F, 4C-E, 6D-E, 7H, 8D, 9H-J, 10I-J, 11)

Coptodactyla subaenea Harold 1877: 40; Matthews 1976: 32.

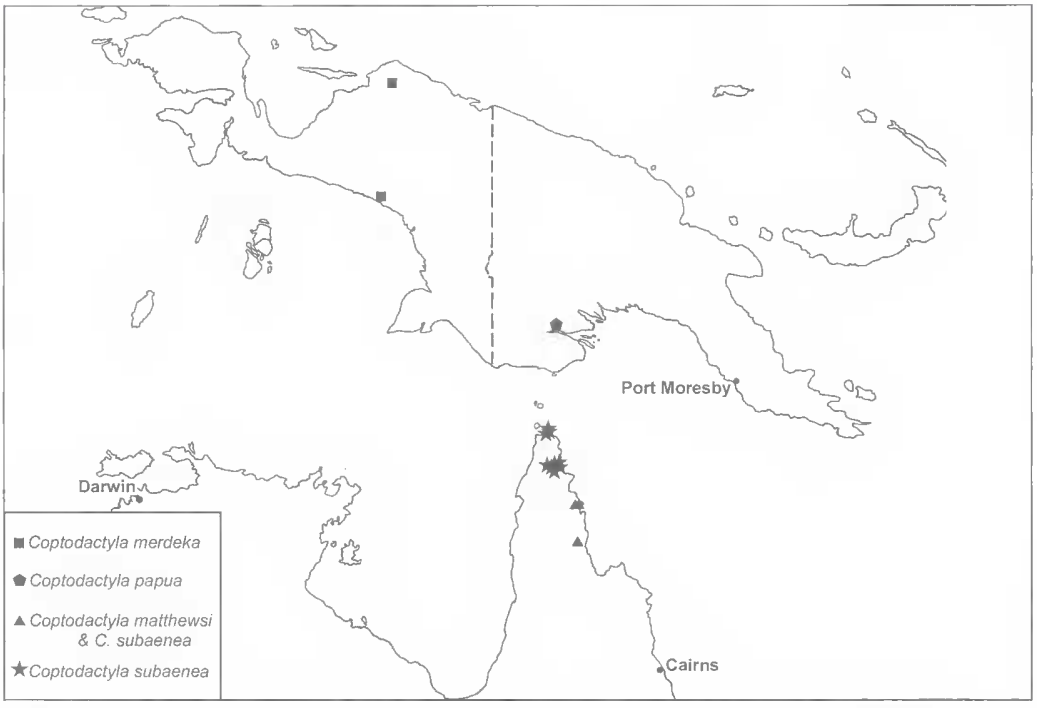

FIG. 11. Map of North Queensland and New Guinea, showing distribution of *Coptodactyla* species.

MATERIAL. QUEENSLAND: Lectotype, ♂ (here designated): labelled: 'Somerset, i.1875, D'Albertis' and 'syntypus *Coptodactyla subaenea* Harold, 1877' (MCG). Paralectotypes (4): 3♂, ♀, same data as lectotype (MCG). Harold did not indicate how many specimens were available for his description. The types listed here are all labelled 'syntypus, *Coptodactyla subaenea* Harold 1877' and two are additionally labelled 'typus'. OTHER MATERIAL. (365) (* = dissected; label data abbreviated to locality, altitude, date, collector): 23*, 11km NW Bald Hill, McIlwraith Ra., 520m, 27.vi-12.vii.1989, TW (ANIC); 1, C. York, ex Macleay Museum (ANIC); 8, Captain Billy Ck, 9-13.vii.1975, GM (QM); 71*, 15km W Captain Billy Ck, 4-9.vii.1975, 5-12.ii.1976, GM (QM); 1, 3km WNW Captain Billy Landing, 3.iv.1993, PZ (ANIC); 23, Cockatoo Ck, 7.ii-23.v.1993, 14.xii.1993-21.i.1994, PZ, Roach (ANIC); 49*, Gordons Mine area, Iron Ra., 12-19.ii.1978, GM (QM); 57*, Heathlands, 15.i-29.ii.1992, 8.xii.1992-19.ii.1993, 24-28.ii.1993, 14.xii.1993, Feeney, TW, PZ (ANIC); 30, 14-15km ENE Heathlands, 15-26.i.1992, 26-28.ii.1993, 14.xii.1993, 19.iii.1994, TW, Calder, PZ (ANIC); 11, 12km NE Heathlands, 15-26.i.1992, TW (ANIC); 11*, 17km NW Heathlands, 15-26.i.1992, 1.iii-25.iv.1992, TW, Feeney, McLeod (ANIC); 14*, 12km SSE Heathlands, 15-26.i.1992, TW, Naumann (ANIC); 1*, Iron Ra., 26.xi.1985, Ferguson (ANIC); 45*, Lake Boronto, Newcastle Bay, 30.i-4.ii.1975, GM (QM); 2*, Leo Ck Rd, McIlwraith Ra., 29.vi-4.vii.1976, GSM (QM); 1*, Lockerbie, 3.iv.1964, Common, Upton (ANIC); 10*, 3-4 km E Lockerbie, 30.i-4.ii.1975, 19-23.iii.1987, GM (QM); 1*, 3km ENE Mt Tozer, 1-4.vii.1986, TW (ANIC); 1*, Quinn Park, Claudie R., 12-21.ii.1985, Edwards, Hacobian (ANIC); 5*, West Claudie R., Iron Ra., 24.v.1974, AWH (CMN).

DIAGNOSIS. Externally identical to *C. nitida* Paulian and *C. storeyi* sp. nov.: pronotal hind angles and sides (lateral to pit and ridge) smooth and finely punctured, without annular punctures (Fig. 1A); disc of elytra not microreticulate; last ventrite impunctate, without conspicuous annular punctures (Fig. 1B); apical lobes of parameres with sharp incurved short spine, blunt tubercle, or slight basal convexity (Figs 2F, 4C-E); lateral sac of endophallus with massive strongly sclerotised spine, 0.75-1 × width of sac (Fig. 6D-E); vulvar sclerite strongly asymmetric, produced above genital opening as a thin quadrate lobe (Figs 8D, 9H-J).

DESCRIPTION. Length 9-13mm.

Head (Fig. 1). Anterior of frontoclypeus wrinkled from line between anterior margins of eyes, including genal angles; posterior half of head moderately strongly and closely punctured,

punctures similar to pronotal disc; ventral clypeal groove deep.

Thorax (Fig. 1). Pronotum rounded at sides; pronotal disc strongly punctured, interspaces 1-2 puncture diameters, micropunctate but shining, without microsculpture, punctures finer and sparser at base; hind angles and sides (lateral to pit and ridge) smooth and finely punctured, without annular punctures; anterior border of pronotum lacking for 0.25-0.4× width of prothorax; base of lateral part of hypomeron without annular punctures; elytra relatively flat in profile; elytra shining, not microreticulate, intervals finely and sparsely punctured, not more obviously at sides; apical half of ventral surfaces of mid and hind femora with annular punctures and fine punctures.

Abdomen (Figs 1B, 7H). Pygidium: shining, not microreticulate, disc finely punctured to impunctate; last ventrite impunctate, without conspicuous annular punctures; internal margin of female pygidial apex shallowly excavate.

Male genitalia (Figs 2F, 4C-D, 6D-E). Apices of parameres strongly deflexed as a flat lobe with small basal convexity, rounded tubercle, sharp inwardly directed triangular tubercle, or curved spur; lateral sac of endophallus with median patch of fine stiff spines, around massive strongly sclerotised spine, 0.75-1 × width of sac; flagellum relatively curved; basal sclerite quadrangular, with strong median fold and basal lobes.

Female genitalia (Figs 8D, 9H-J, 10I-J). Dorsal sclerite flat and broad, without sharp transverse ridge; vulvar sclerite strongly asymmetric, produced above genital opening as a sharp quadrate lobe above deep oblique groove and beside broad folded cavity; spermatheca relatively small.

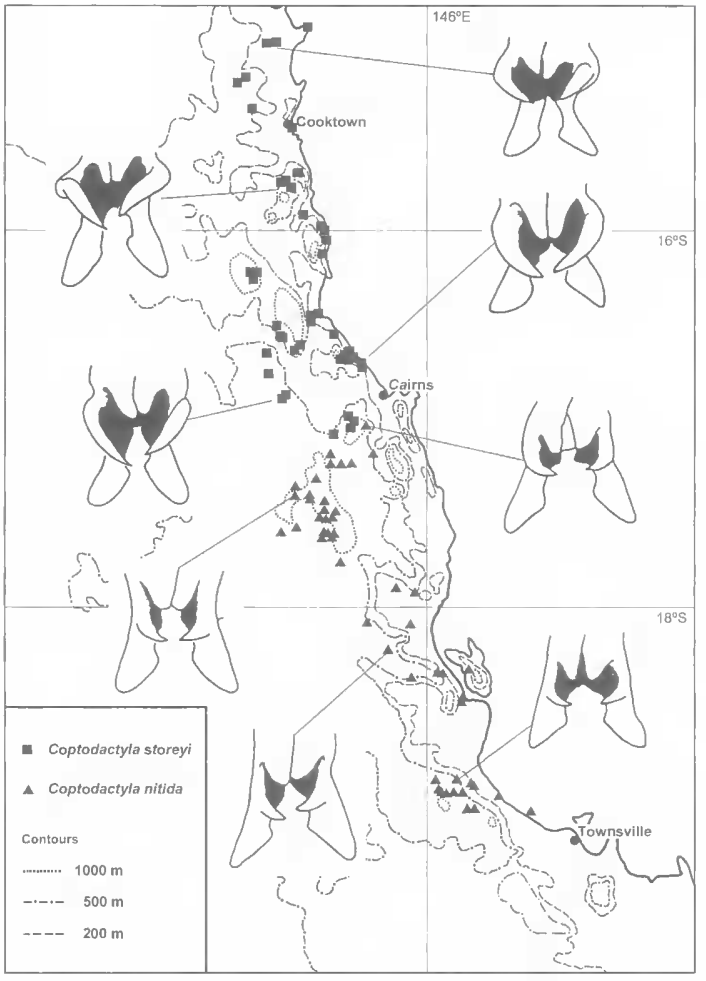

FIG. 12. Map of North Queensland, showing distribution of *Coptodactyla nitida* and *C. storeyi* with shape of paramere apices at various sites.

Intraspecific variation. There is variation in the shape of the paramere lobes (Figs 2F, 4C-E), including the angulation of the inner margin and the size of the tubercles. In the northern populations the parameres are almost identical to those of *C. nitida*, but in southern populations (Iron Range and McIlwraith Range) the tubercles are reduced to triangular points, small bumps, or are absent, as noted by Matthews (1976). The vulvar sclerite also varies (Figs 8D, 9H-J), but consistently has a large sharp quadrate lobe above a deep oblique groove, beside a broad shallow pouch. There appear to be no consistent differences, between northern and southern

populations, in either the endophallus (Fig. 6D-E) or female genitalia.

REMARKS. Harold's type material (in MCG, not Museum of Natural History, Paris (Matthews, 1976; Cassis & Weir 1992)) has been examined and a male and a female paralectotype dissected to fix the identity of this species (Figs 4D, 9H). The shape of the parameres is variable and the apices (usually diagnostic in *Coptodactyla*) may be almost identical to those of the allopatric *C. storeyi*, but the structures of the endophallus and vulvar plate are consistently different.

Coptodactyla subaenea is the only member of the complex known from the northern tip of Cape York Peninsula, but is sympatric with *C. matthewsi* to the south, in the Iron and McIllwraith Ranges, where the two species occasionally occur together (Fig. 11). It has been collected from human and dingo dung, rotting bananas and fungi, yellow pan traps, flight traps and at light. It occurs commonly in a range of habitats, including scrub heath, open forest and rainforest, from 0 to 520m above sea-level. Specimens have been collected in every month from November (once) to July, except June.

DISCUSSION

Six species are discriminated here from 1,750 specimens of *Coptodactyla*, which had been confused under the names *C. papua* and *C. subaenea*. External characters allow identification of three taxa: the *C. merdeka*/*C. papua* pair, *C. matthewsi* and the complex of *C. nitida*/*C. storeyi*/*C. subaenea*. The structure of the parameres (Figs 2C-F, 3, 4) separates all species except *C. nitida*/*C. subaenea*, whereas the structure of the endophallus (Figs 5B-E, 6) separates all species except *C. nitida*/*C. storeyi*. The vulvar sclerites may be diagnostic for each species (Figs 8-9), but the difference between *C. merdeka* and *C. papua* is based on two specimens, and the difference between *C. nitida* and *C. storeyi* is slight. The spermatheca is almost identical in all species (Fig. 10). The traditional external and male genitalic characters fail to discriminate two species, *C. nitida* and *C. subaenea*, which are easily distinguished by the endophallus and vulvar sclerites.

PHYLOGENETIC ANALYSIS. The *subaenea* species-complex is a monophyletic group within *Coptodactyla*, defined by two synapomorphies: lack of complete anterior pronotal border and lack of male secondary sexual characters. A small set of cladistically varying, mostly primary sexual, characters (Table 1), was found for this species-complex and polarised by reference to all other species of *Coptodactyla* (all 0 states for Table 1). Parsimony analysis of this set produced three minimum-length trees with lack of resolution of the -(*nitida*, *storeyi*, *subaenea*) clade. This clade may be resolved on similarity criteria, as *C. nitida* and *C. storeyi* are almost indistinguishable in both male and female primary sexual characters, giving a single phylogenetic hypothesis (Fig. 13).

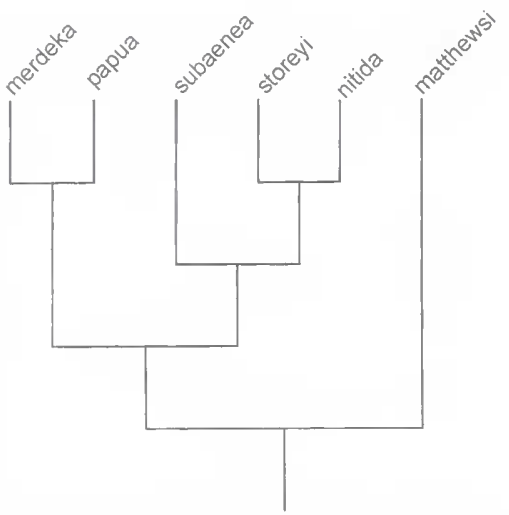

FIG. 13. Cladogram of *Coptodactyla subaenea* species-complex, based on characters listed in Table 1, polarised by comparison with other species of *Coptodactyla*.

BIOGEOGRAPHY. The two sister (or at least most similar) species, *C. nitida* and *C. storeyi*, are only separated by proportional differences in the parameres and vulvar sclerites. Nevertheless, separation of the specimens using these characters shows two adjacent allopatric distributions in the Wet Tropics of north Queensland, with the boundary approximately between Mareeba and Atherton (Fig. 12). This boundary is at the southern edge of the Black Mountain Barrier (BMB), a well known region of population disjunction in vertebrates (Joseph et al. 1995; Schneider et al. 1998). The BMB was a broad swathe of low-rainfall woodland at various periods of late Tertiary and Pleistocene maximum aridity, separating blocks of rainforest to north and south (Nix & Switzer 1991; Hopkins et al. 1996) and a likely precursor to speciation in rainforest taxa. In the *C. nitida*/*storeyi* species

pair, soil moisture is probably as much a limiting factor as forest type, as both occur in a broad range of the latter, including open woodland, but are only active in the wetter months of the year. For these species, at times of high aridity, the low rainfall of the BMB provided a soil barrier together with probable absence of closed forest. The coincidence of the distributions of the weakly discriminated *C. nitida* and *C. storeyi* with a known historical geographic barrier supports recognition of these taxa as species. No males with intermediate genitalia have been seen, but there are two indeterminate female specimens, both from the north-west slopes of the Lamb Range (Clohesy River and Davies Creek), at the junction of the two species.

At present, it is not known what maintains the narrow boundary of the species *C. nitida* and *C. storeyi*, although it does not appear to be edaphic factors as both species occupy similar climatic space (Reid et al., in press). The relative lack of variation in paramere and vulvar sclerites in these species, compared with *C. subaenea*, may indicate that a significant part of species-discrimination occurs during attempted copulation. This may partly explain sympatry of *C. matthewsi* and *C. subaenea*, which are relatively phylogenetically distant and have the most divergent male and female genitalia.

KEY TO SPECIES OF *COPTODACTYLA* BURMEISTER

(modified from Matthews (1976); abbreviations used in key: NG = New Guinea; CQ, NQ, SQ = central, north and south Queensland; NT = Northern Territory)

1. Angular or arcuate ridge on underside of clypeal margin accompanied by a narrow groove for more than half width; median lobe of metasternum without anterior depression; both sexes without cephalic or pronotal armature 2

   Underside of clypeal margin with small transverse or round pit or this absent; median lobe of metasternum with shallow depression in middle of anterior; major male with horn on head and usually anterior pronotal folds 10

2(1). Pronotum with middle of anterior border effaced (Figs 1A, 2A-B); without sexual dimorphism of legs 3

   Anterior pronotal border complete, except worn specimens of *C. depressa* Paulian, in which pronotum lacks basal row of sensory punctures and 8th and 9th striae do not reach elytral base; male femur with posterior marginal ridge interrupted at base 8

3(2). Annular punctures present at hind angles of pronotum and along lateral edges; each paramere with long thin spur at middle of apical lobe, overlapping other paramere or almost so (Fig. 3B,E); apex of female pygidium deeply excavate, lobes externally directed (Fig. 7D-E) (lateral lobe of endophallus with minute apical spine or spine absent (Figs 5C, 6A); vulvar sclerite almost symmetrical, without sharp lobe (Figs 9B,E)) (NG) 4

   Hind angles of pronotum and basal half of lateral margins smooth, almost impunctate, without annular punctures (rarely 1-3 present) (Fig. 1A); each paramere with thick slightly incurved spine at base of apical lobe (Fig. 2D-F), or apical lobes straight and elongate (Fig. 2C); if apex of female pygidium deeply excavate, lobes internally directed (NQ) 5

4(3). Sides of parameres deeply hollowed, bounded by sharp longitudinal ridge (Fig. 3D), apical spurs of parameres produced; lateral lobe of endophallus without sclerite (Fig. 6A); ridge of vulvar sclerite less strong, angular (Fig. 9E) . . . . . *papua* Lansberge

   Sides of parameres not deeply hollowed, without longitudinal ridge (Fig. 3B), apical spurs tightly overlapping lobes; lateral lobe of endophallus with minute sclerite (Fig. 5C); vulvar sclerite more strongly ridged, convex (Fig. 9B) . . . . . *merdeka* sp. nov.

5(3). Genal angles finely punctured, almost impunctate, smooth (Fig. 2A); elytral disc densely microreticulate, contrasting with shining suture and lateral intervals; parameres with straight elongate apical lobes, without incurved spines (Figs 2C, 3A); lateral lobe of endophallus without apical spine (Figs 5B); apex of female pygidium (Fig. 7C) deeply excavate, lobes internally directed; vulvar sclerite almost symmetrical, without sharp lobe (Figs 8A, 9A) (Iron & McIlwraith Ranges) . . . . . *matthewsi* sp. nov.

   Genal angles strongly punctured, transversely rugose, as anterior of frontoclypeus but less wrinkled (Fig. 2B); elytra not microreticulate (old specimens may be densely scratched and dull); apical lobes of parameres usually with incurved basal spines (spines may be reduced to small tubercles; Figs 2D-F, 4C-E); endophallus with prominent spine (Fig. 6B-E); apex of female pygidium shallowly excavate (Fig. 7F-H); vulvar sclerite with asymmetric sharp lobe (Fig. 8B-D) 6

6(4). Apex of parameres with short triangular or blunt tubercle, or without tubercle, at base of apical lobe (Figs 2F, 4C-E); lateral lobe of endophallus with massive apical spine, 0.75-1 × width of sac (Fig. 6D-E); vulvar sclerite with large sharp lobe, quadrate in shape (Figs 8D, 9H-J) (tip of Cape York Peninsula south to Iron & McIlwraith Ranges) . . . . . *subaenea* Harold

   Apex of parameres with larger sharply pointed basal spur (Fig. 2D-E); endophallus with smaller spine, 0.3-0.5 × width of sac (Figs 5D-E, 6B-C); vulvar sclerite with smaller triangular or rounded lobe (Fig. 8B-C) 7

7(6). Apical lobe of parameres with large down-curved spurs (Figs 2E, 4A-B, 12); vulvar sclerite with triangular sharper lobe (Figs 8C, 9F-G) (Cape Flattery south to Cairns and Mareeba) . . . . . *storeyi* sp. nov.

   Apex of paramere with short incurved spur at base of lobe (Figs 2D, 3C-D, 12); lobe of vulvar sclerite more rounded in profile (Figs 8B, 9C-D) (Mareeba south to Paluma) . . . . . *nitida* Paulian

8(2). 8th and 9th elytral striae effaced at base, 9th for at least basal quarter; male without spur on fore tibia; elytral striae impunctate and elytra without pseudepipleura (NQ) . . . . . *depressa* Paulian

   8th and 9th striae complete or almost so; male with median spur on fore tibia 9

9(8). 9th elytral interval evenly rounded; elytral striae strongly punctate; lateral carina of pronotum from

margin to lateral depression, sharp (SQ) . . . . . *meridionalis* Matthews

9th elytral interval strongly recurved, at least for apical 3/4, forming pseudepipleuron; elytral striae impunctate or almost so; lateral carina of pronotum obsolete (C&NQ) . . . . . *onitoides* Gillet

10(1). Ridge on underside of clypeus without pit; femora impunctate; length 15-18mm & striae impunctate (NQ) . . . . . *ducalis* Blackburn

Ridge with pit; femora with a few punctures; if length >14mm striae punctate 11

11(10). Lateral carina of pronotum completely sharp; striae with large punctures with raised centres 12

Lateral carina of pronotum effaced before fossa; striae impunctate or finely punctured. 14

12(11). Basal fifth of 8th stria missing; anterior of pronotal disc impunctate; male without pronotal tubercles or folds (NQ, NT) . . . . . *glabricollis* (Hope)

8th stria complete or almost so; female with anterior of pronotal disc closely punctate; male with pronotal tubercles or folds 13

13(12). Ridge on underside of clypeus with transverse groove; major male with simple anterior pronotal excavation (NT) . . . . . *lesnei* Paulian

Ridge with minute pit; major male with row of transverse wrinkles at sides of anterior pronotal excavation (NT) . . . . . *stereocera* Gillet

14(11). Elytral striae complete to base; female with 2 faint depressions on anterior of pronotal disc; major male with pair of blunt tubercles at top of anterior pronotal excavation and tip of cephalic horn not expanded or secondarily lobed (NQ) . . . . . *brooksi* Matthews

8th stria effaced before base; female without depressions; major male with tip of cephalic horn expanded or secondarily lobed 15

15(14). Major male: cephalic horn long and narrow and secondarily lobed at tip; pronotal median groove present 16

Major male: cephalic horn short and broad, with flat explanate tip; pronotal tubercles single, widely separated and without groove between (NQ) . *torresica* Matthews

16(15). Major male: cephalic horn long & narrow, with concave quadrituberculate tip, anterior and basal tubercles more strongly raised, but all small and evenly convex; tubercles above anterior pronotal excavation bifid with deep hollow between (NQ) . . . . . *monstrosa* Felsche

Major male: frontoclypeal horn long & narrow, with bituberculate apex, anterior tubercle small and hollowed, posterior broad and bidentate at tip; pronotal anterior with two transverse depressions, subcarinate above these and with shallow median groove (NG) . . . . . *tuberculata* Gillet

TABLE 1. Characters used for cladistic analysis of *Coptodactyla subaenea* species-complex.

1. Front margin pronotum. ***0.*** complete. ***1.*** medially absent.

2. Annular punctures. ***0.*** absent from lateral pronotal margins. ***1.*** present throughout.

3. Males. ***0.*** with secondary sexual modifications. ***1.*** without.

4. Tips of parameres. ***0.*** deflected, without median tubercles or spurs. ***1.*** with basal tubercles or short thickened median spurs. ***2.*** apical thin elongate spurs.

5. Parameres. ***0.*** not laterally keeled. ***1.*** at least keeled at base of deflexed apical lobes.

6. Endophallic lateral sac. ***0.*** without prominent triangular spine. ***1.*** with.

7. Endophallic basal sclerite. ***0.*** with lateral lobes and several folds. ***1.*** with single median fold.

8. Internal lobes apical margin female pygidium. ***0.*** prominent. ***1.*** reduced.

9. Vulvar sclerite. ***0.*** symmetrical. ***1.*** strongly asymmetric with prominent lobe.

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